DIRECT EVIDENCE FOR TRADE-OFFS BETWEEN FORAGING AND GROWTH IN A JUVENILE SPIDER

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ABSTRACT. A simple modification of classical optimal foraging models yields explicit predictions of the allocation of resources to orb-web synthesis and weight gain in a spider. Because the spiders may be trying to avoid weight loss, weight gain and web size are predicted to be be negatively correlated at higher food levels and positively correlated at lower food levels. These predictions were upheld qualitatively by experiments involving juvenile *Nephila clavipes* and *N. maculata*.

RESUMEN. Una sincilla modificación a los modelos clásicos del forrajeo óptimo da predicciones explícitas sobre la repartición de recursos entre el sintesis de la tela orbicular y el aumento de peso en una araña. Dado que arañas posiblemente están ententando evitar la pérdida de peso, la interacción entre el aumento de peso y el tamaño de la tela debería estar negativamente correlacionada bajo majores niveles de alimentación, y positivamente correlacionada bajo de condiciones de alimentación reducida. Estas predicciones fueron appoyadas experimentalmente utilizando juveniles de *Nephila clavipes* y *N. maculata*.

Classical foraging models are based on the assumption that optimal allocation of limiting resources among various expenditures increases the fitness of the organism either directly (through increased reproductive success) or indirectly (through increased growth) (e. g., Schoener 1971; Pyke et al. 1977; Mangel & Clark 1986). Despite the key role of this assumption, few studies have described the interaction between foraging investment and growth at different levels of food availability. This appears in part due to the difficulty of finding common units of measure (Pianka 1981; Stephens & Krebs 1986). If common resources are used for both growth and foraging, then explicit predictions can be made concerning their allocation at different levels of prey availability.

The study of foraging in orb-web building spiders allows observation of resource allocation because foraging investment is measurable as material investment into the web, and the orb is composed of physiologically important compounds. The orb web is renewed regularly, and changes in orb-web size reflect the response of the spider to foraging conditions (Buskirk 1975; Gillespie 1987; Higgins & Buskirk 1992). The viscid silk that forms the spiral of the orb is a protein thread coated with a mixture of organic compounds that also have physiological functions (Tillinghast 1984; Dadd 1985; Townley et

al. 1991). Thus, construction of each orb requires decisions concerning the allocation of metabolically important compounds; such decisions could directly affect growth.

In some large araneoid spiders, fitness is increased by rapid development and weight loss is predicted to reduce the fitness of the females (Higgins & Rankin, in press). The existence of resources common to both foraging and growth and the fitness penalties associated with weight loss imply that when resources are limiting, foraging behavior might be different from that predicted by foraging models calculating maximization of the rate of energy intake. Here, I present a simple model that predicts patterns of allocation of resources between foraging and weight gain at food levels varying from very low to very high. I experimentally tested this model using juvenile *Nephila clavipes* (L.) and *N. maculata* (Fabr.) (Araneae: Tetragnathidae) that were fed at very low, intermediate and high levels.

THE MODEL

If it is true that the functions of weight gain and web building are competing for common resources and if it is important to the individual to avoid weight loss, a simple modification of the classic foraging investment models (Schoener 1971) is necessary to predict behavior at very low levels of prey availability. The model is pre-
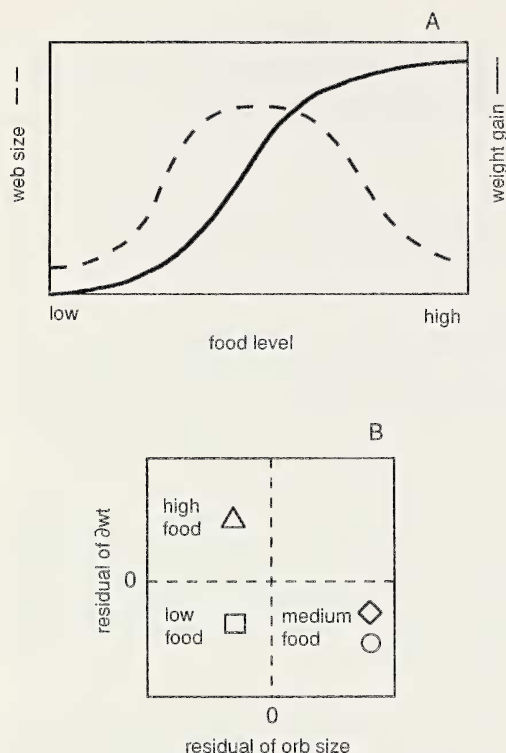
Figure 1.—The model of resource allocation by an orb-weaving spider. **A.** As food resources increase for a given individual, orb size increases then declines and weight gain increases. **B.** Among spiders, the residuals of orb size and weight gain regressed against spider size are compared (eliminating the variation due to spider size). At low food levels (square), orb size and weight gain are lower than average; at medium food levels (circle, diamond), orb size is greater and weight gain is lower than average; and at high food levels (triangle), orb size is lower and weight gain is higher than average.

sented graphically in Fig. 1. At high to intermediate levels of food, the spiders have sufficient resources to avoid weight loss and increase investment into foraging as food levels decrease. This is consistent with classical foraging models: as average foraging success decreases, the investment into hunting (e. g., searching time per patch) is predicted to increase (maximizing energy gain/effort; Stephens & Krebs 1986). If common resources are being allocated into growth and foraging then the rate of weight gain will be slower, due to both decreased prey capture and increased foraging investment. However, this prediction will not hold at lower food levels if the spiders must avoid weight loss. When resources are so limiting that weight loss would be the price of continued increases in foraging in-

vestment, the spiders should reduce their foraging effort. Thus, the relationship between weight gain and web investment in spiders is predicted to be negatively correlated at higher food levels, and positively correlated lower food levels.

METHODS

In order to test the prediction that the relative investment into the orb and weight gain will differ between the shift from very low to intermediate foraging success and the shift from intermediate to high foraging success, I controlled prey availability in juveniles of two species of *Nephila*: lab-reared *N. clavipes* in Panama and field-collected *N. maculata* in Madang, Papua New Guinea. In both cases the investment into weight gain and orb area were recorded as functions of prey availability, measured as the daily prey weight/initial spider weight.

The basic methods were the same in the two experiments. To control the structural environment used in web construction, I placed individuals on 30 cm diameter spherical frames consisting of two hoops of 3 mm × 6 mm fiberglass, fixed at right angles and suspended from the ceiling or braces in open-air insectaries. I fed spiders locally available stingless bees (*Trigona* sp.), a common prey item of these spiders (Higgins & Buskirk 1992; Higgins, pers. obs.). Bees were collected from the same nests throughout the experiment.

For each animal, I recorded daily orb-web area and rate of weight gain. (Mesh size, measured as the number of spiral strands per 2 cm (Higgins & Buskirk 1992), did not vary with food level in either species. *N. clavipes*: $F_{(1, 34)} = 3.16$, *ns*; *N. maculata*: $F_{(2, 13)} = 0.34$, *ns*). Orbs built by these spiders are asymmetrical, and orb-web area was estimated as a half ellipse using measurements of the vertical and horizontal radii. While many orb weavers replace the orb each day, these spiders sometimes only partially renew the orb (Lubin 1973). When a web was partially new, the area was estimated by calculating the area of the orb then reducing to the estimated area that was new ($\leq\frac{1}{3}$, $\leq\frac{1}{2}$, $\leq\frac{2}{3}$, $\leq\frac{3}{4}$). Orbs are not of constant size during the intermolt interval (Higgins 1990), therefore, foraging investment was measured as the mean area of all orbs spun during the intermolt period. If a spider did not molt during the experiment, the mean area during the experiment was used.

Web size and rate of weight gain are both functions of spider size. Spider size was measured as
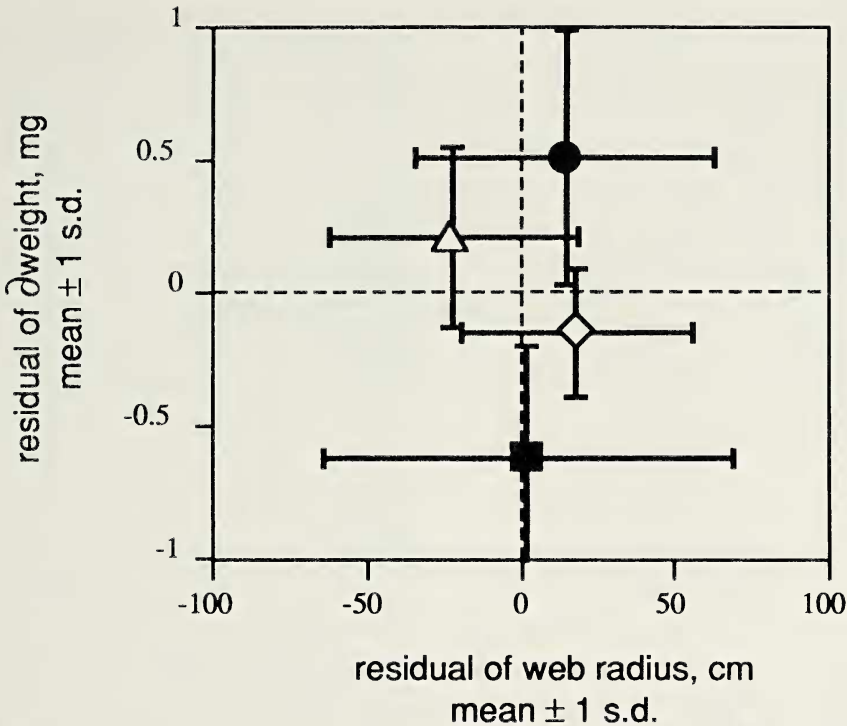
Figure 2.—The relationship between mean orb-web size and mean daily weight gain in *Nephila clavipes* under three different food levels (% initial spider weight), two trials. Trial 1 (filled symbols): diamond – 20%, triangle – 35%. Trial 2 (open symbols): square – 10%, circle – 20%.

the length of the leg I tibia + patella length, cm (TPL), which does not vary between molts. Spider weight, which increases between molts, can be estimated from TPL and abdomen volume (Higgins 1992a; the same equation was used for both species). The rate of weight gain in mg was calculated for all spiders as δwt mg (= wt_{Final} – $\delta wt_{Initial}$/no. days observed). To eliminate the influence of size, the residuals of web size and weight gain regressed against spider size were the dependent variables in the statistical analyses. Multivariate analysis of variance (MANOVA) allowed simultaneous comparison of the effects of prey level on the rate of weight gain and web size. When the MANOVA was significant, as indicated by Wilks' lambda, ANOVA were used to examine the variation in each dependent variable.

Nephila clavipes.—For this experiment, I raised spiders from both generations of a bivoltine population on Barro Colorado Island, Panama. First-generation females mature in the early rainy season (May-June), and second generation females mature as the rains end (December-January) (Higgins 1992a). Eggs were collected from two

gravid females of each generation. The first two cohorts of spiderlings hatched in January, and the second two cohorts hatched in May of 1986, resulting in two separate trials. Each cohort was kept in a fine-screened cage (15 cm w. × 30 cm l. × 60 cm h.) within an open-air, screened insectary, and large numbers of field-caught *Drosophila* spp. were released into the cages twice daily. As each spider reached the third instar, it was removed from the common cage, marked and placed onto a spherical frame. During this instar, each spider was offered one stingless bee daily (mean weight 3.5 mg, mean body length 4 mm).

The experimental treatment was initiated in either the fourth (first trial) or fifth (second trial) instar. Within each trial, the spiders were fed either two or one stingless bees daily, the mean number of prey captured per day in the field in the rainy and dry seasons, respectively (Higgins & Buskirk 1992). As each spider molted, it was measured (TPL, abdomen length and width, cm), individually marked with Testors® enamel paint, and randomly assigned to receive one or two bees/day. Penultimate-instar males may parti-
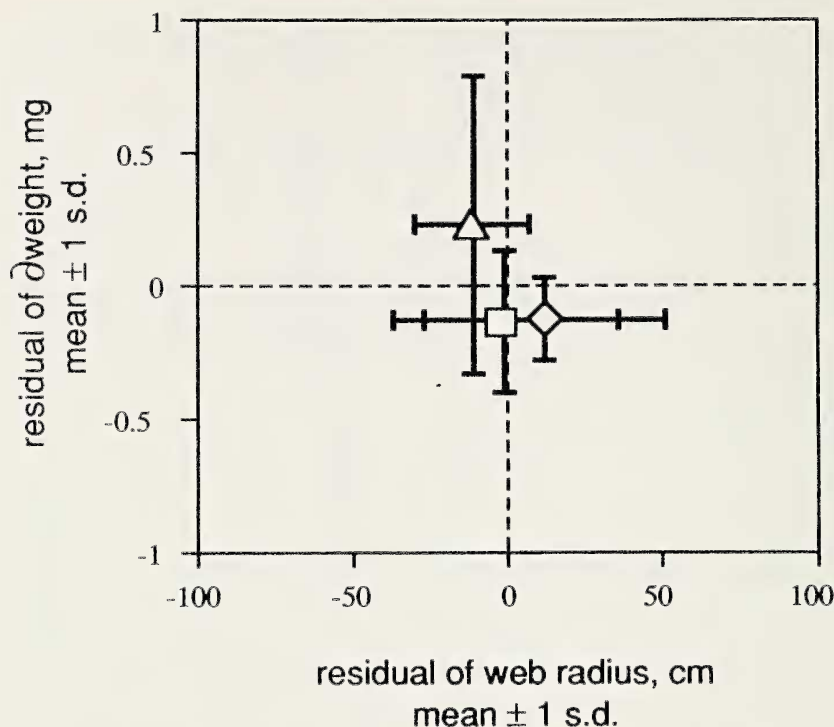
Figure 3.—The relationship between mean orb-web size and mean daily weight gain in *Nephila maculata* under three different relative food levels (% initial spider weight). square: <17%; triangle: <22%; diamond: <45%.

tion resources differently (Higgins 1993); therefore, males in this instar were not used in the experiments. Treatment lasted 14 days, slightly longer than the mean intermolt interval of the fourth instar. If, at any time, an individual moved off its frame, the support strands of the new web were carefully cut and the spider with its web was placed back onto the frame, after measurements (after M. Robinson, pers. comm.). Movement off of the frames occurred with equivalent frequency in all groups (test for full independence: $G = 6.61$, $df = 4$, *ns*; Sokal & Rohlf 1981).

The experimental treatment was started on average one instar later in the second trial. Because of the difference in instar between the two trials, the spiders differed in initial size and weight. Therefore, the two treatments (1 *vs.* 2 prey/day) yielded three levels of prey weight relative to initial spider weight: high (35%) and medium (20%) in the first trial, medium (20%) and low (10%) in the second. One individual's relative food weight was 26%; preliminary analyses indicated no difference in the statistical outcome when it was included in the medium or high group, so it was assigned to the former.

The regressions of orb area and rate of weight gain against spider size were significant (orb area = $166.6 + 521.6$ (TPL); $R^2 = 0.57$, $F_{(1,36)} = 48.81$, $P < 0.001$; ln(δwt) = $-1.82 + 2.80$ (TPL), $R^2 = 0.09$, $F_{(1,34)} = 3.53$, *ns*). Insufficient spiders survived to allow examination of variation among clutches, but the spiders of both clutches were assigned to each treatment within a trial, controlling for this factor.

Nephila maculata.—In February and March of 1993, I conducted a similar experiment with *N. maculata*. Small groups (no more than 10 at a time) of second -- fifth instar spiders from the forests of Baitabag village, west of Madang, Papua New Guinea, were held indoors overnight to encourage building on the frames. Afterwards, the spiders were moved to a screened, roofed insectary, and randomly assigned to a diet (low or high). The number of prey items was adjusted according to spider instar. I fed second and third instar spiders *Drosophila* spp.(0.67 mg each; low = 2/day, high = 4/day (second instar) or 6/day (third instar)), and larger spiders *Trigona* bees (5 mg each; low = 1/day, high = 2/day). The experimental treatment was continued for 10 days,

after which the spiders were returned to the forest and new individuals were collected. The shorter interval reflects both the shorter intermolt duration of this species, and the need to maximize the number of animals used in the experiment. Although I had randomly assigned prey availability, I could not make the spiders eat and prey consumption was highly variable. Therefore, the independent variable used in the statistical analyses is the relative mean weight of prey actually eaten (presented as % initial spider weight). The continuous distribution of prey consumed was divided into three approximately equal groups of increasing relative prey weight.

N. maculata were not as likely as *N. clavipes* to build an orb each day, perhaps due to the insectary being roofed. Therefore, the foraging investment reported is the total area of orb built during the experiment divided by the number of days hunting (determined as the number of days with a new orb plus the number of days that the spiders accepted prey although a new orb had not been built). The size range of spiders used was larger than in the previous experiment, so the data had to be transformed to correct for heteroscedasticity prior to statistical analysis of the residuals (ln (δwt) = $-0.997 + 2.698$ (TPL), $R^2 = 0.33$, $F_{(1,15)} = 7.398$, $P < 0.025$; (web/hunt)$^{1/2}$ = $8.506 + 10.67$ (TPL), $R^2 = 0.34$, $F_{(1,15)} = 8.26$, $P < 0.025$).

RESULTS

***Nephila clavipes*.**—Both rate of weight gain (δwt) and mean orb size varied with food level (Fig. 2). From 10% to 20% relative food (second trial), δwt and orb size increased, while from 20% to 35% relative food (first trial), δwt increased and orb size decreased. Three MANOVA compared the responses of the spiders to food level within each trial, and compared between trials at the 20% food level; the significance levels were adjusted for multiple, non-independent tests. In the second trial, there was a significant effect of food level on δwt but not on web size (Wilks' λ = 0.356, $P < 0.01$; ANOVA: δwt: $F_{(1, 13)} = 23.5$, $P < 0.001$; web size: $F_{(1, 13)} = 0.20$, *ns*). There was a significant effect in the first trial on both web size and δwt (Wilks' λ = 0.568, $P < 0.01$; ANOVA: δwt: $F_{(1, 19)} = 8.09$, $P = 0.01$; web size: $F_{(1, 19)} = 5.41$, $P = 0.03$). Between trials, there was a significant difference in δwt but not web size (Wilks' λ = 0.514, $P < 0.01$; ANOVA δwt: $F_{(1, 17)} = 16.05$, $P < 0.01$; web size: $F_{(1, 17)} = 0.03$, *ns*). The effect of trial in the medium food level
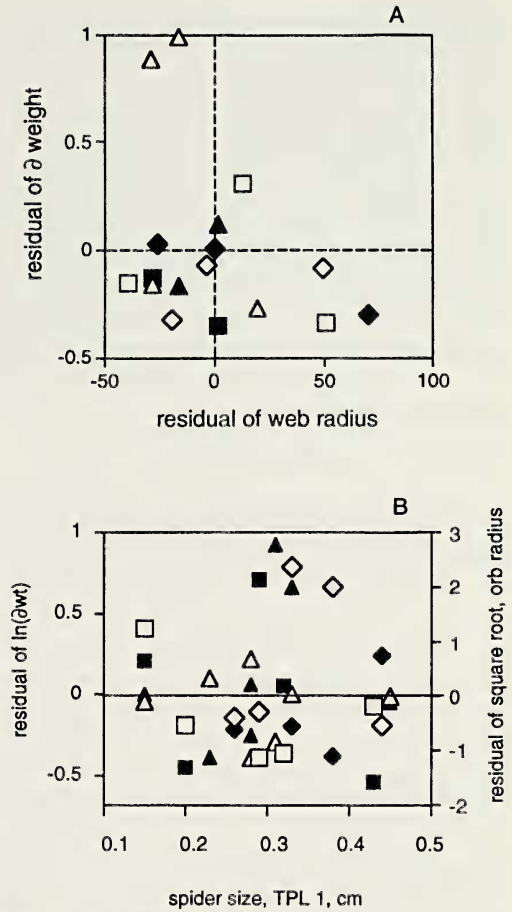
Figure 4.—The relationship between mean orb-web size and mean daily weight gain in individual *Nephila maculata* under three different food levels (% initial spider weight). Square – <17%, triangle – <22%, diamond– <45%. **A.** There is no effect of the sex of the individual on resource allocation. Male = filled symbols, female = open symbols. **B.** There is no effect of initial spider size on resource allocation. Filled symbols = residual of orb-web size, open symbols = residual of δwt.

is probably due to the larger mean initial spider size in trial 2.

Reduced rate of weight gain had a significant negative effect on the development rate of the spiders, observed as an increase in the number of days between molts. Eighteen spiders from trial 1 were held on the assigned diet until they molted and the number of days between molts was correlated with the rate of weight gain and initial spider size (ln (days between molts) = 1.96 $- 37.7$ (δwt) + 4.81 (TPL); $R^2 = 0.46$, $F_{(2, 15)} = 6.25$, $P = 0.011$; only 5 spiders molted in trial 2).

Nephila maculata.—Although the pattern of variation in orb investment and rate of weight gain among the three groups is similar to that observed for *N. clavipes*, the differences are not significant (Fig. 3; Wilks' $\lambda = 0.78$, $P = 0.5$). What is most striking is the variation among individuals in response to the same level of food intake (Fig. 4). Often, different individuals made opposite responses: one spider building larger-than-average orbs and gaining little weight, another building smaller-than-average orbs and gaining weight rapidly. The variation was not a function of the sex nor of the initial size (TPL) of the individual (Fig. 4).

CONCLUSIONS

The two experiments uphold the predictions of the model. Juvenile *Nephila* of both species tended to increase orb-web size and decrease the rate of weight gain with slightly reduced prey capture; they decreased both orb-web size and rate of weight gain in response to greater reductions in prey capture. This response resulted in the counter-intuitive pattern of decreased foraging investment with low food availability, upholding the initial assumptions that resource allocation is constrained by a need to avoid weight loss and that common resources are used in foraging and growth in these spiders. At very low food levels, webs were small and few spiders gained weight but none lost weight. This food level is within the range captured in Panama, but much lower than median prey capture rates observed in Madang (4 prey/12 h diurnal observation) (Higgins & Buskirk 1992; Higgins, pers. obs.).

Nephila maculata juveniles varied greatly in their response to the experimental treatment. Such differences were not found in the experiment with *N. clavipes*, when the spiders were reared under homogeneous conditions. This difference might represent some intrinsic difference between species, but probably reflects differences in experience prior to the experiment. *N. maculata* juveniles were collected in the field, and undoubtedly differed in their foraging histories. The foraging history of an individual may cause it to respond in a particular fashion to changes in prey capture rates. This implies differences in the response to short *vs.* long term variation in prey capture, which cannot be examined by the short-term experiments presented here.

There is evidence that many spiders evolved under conditions of food limitation (Anderson 1974; Wise 1975, 1979). In web-building spiders, the web must be built before the foraging quality of a site can be assessed. Perhaps due to this initial investment, or due to temporal variation in prey availability, many web-building spiders are highly site-tenacious (Eberhard 1971; Enders 1976; Tanaka 1989; however, see Turnbull 1964). Rather than abandoning poor patches, a strategy often predicted by foraging theory (e. g., Charnov 1971; Pyke et al. 1977), spiders show other behavioral and physiological responses to nutritional stress (Riechert & Luczak 1982; Sherman 1994). However, these responses can slow growth and affect both survival and female fecundity (Higgins 1992a, 1992b, pers. obs.). The results of these studies support the hypothesis that there are potentially limiting resources necessary for both orb silk synthesis and growth, predicted by the chemical analyses of orb-silk by Tillinghast and Townley (Tillinghast 1984; Townley et al. 1991). The spiders must invest in the orb web in order to capture prey, but unless critical resources are in abundance, such investment necessarily delays growth and development and potentially compromises individual fitness. Predation rate declines with increasing spider size and fecundity increases with early maturation (Higgins 1992b, pers. obs.), so lengthening time between molts can have a detrimental effect on fitness. To avoid reduction in weight during periods of low food availability, the interactions between foraging investment and growth may be more complex than predicted by classical optimal foraging models.

ACKNOWLEDGMENTS

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